

Systematics of the fossil arachnids

Jason A. DUNLOP

Department of Earth Sciences
University of Manchester
Manchester M13 9PL, U.K.

Systematics of the fossil arachnids. - Previous systematic accounts of the extinct, fossil arachnid orders Anthracomartida Karsch, 1882, Phalangiotarbida Haase, 1890, Haptopoda Pocock, 1911, Kustarachnida Petrunkevitch, 1913 and Trigonotarbida Petrunkevitch, 1949 are reviewed. The subclasses Soluta Petrunkevitch, 1949 and Stethostomata Petrunkevitch, 1949 are rejected. Anthracomartida is synonymised with Trigonotarbida, which is placed in Tetrapulmonata Shultz, 1990. Kustarachnida represent misidentified opilionids. The position of the remaining extinct orders, Phalangiotarbida and Haptopoda, remains obscure, though Phalangiotarbida resemble opilioacarid mites and Haptopoda may belong in Tetrapulmonata.

Key-words: Arachnid - systematics - Anthracomartida - Haptopoda - Phalangiotarbida - Kustarachnida - Trigonotarbida - Soluta - Stethostomata - Tetrapulmonata.

INTRODUCTION

The arachnid orders (considering Arachnida as defined by WEYGOLDT & PAULUS (1979) and SHULTZ (1990)) which are extinct and therefore known only from fossils are the Anthracomartida Karsch, 1882, Phalangiotarbida Haase, 1890, Haptopoda Pocock, 1911, Kustarachnida Petrunkevitch, 1913 and Trigonotarbida Petrunkevitch, 1949. Some earlier studies of arachnid phylogeny included these fossil orders (see below), though reached few concensuses over their position. However, the three principal recent arachnid phylogenies (WEYGOLDT & PAULUS 1979; VAN DER HAMMEN 1989; SHULTZ 1990) did not formally place the fossil orders in their schemes, partly as a result of the characters defining these orders not being as well

Manuscript accepted 02.09.1995.

Proceedings of the XIIIth International Congress of Arachnology, Geneva, 3-8.IX.1995.

established in comparison to their extant relatives. This problem is compounded by the efforts of PETRUNKEVITCH (1913, 1945, 1949, 1953, 1955) who dominated fossil arachnid work in his day, yet made erroneous observations and questionable interpretations and systematic referrals of the fossil material (see SELDEN (1993) for criticisms of Petrunkevitch's methods and conclusions). This present study critically reviews previous systematic referrals of the fossil arachnid orders.

MATERIALS AND METHODS

Specimens of fossil arachnids were reviewed primarily from the collections of the British Museum (Natural History) (BMNH) and the Smithsonian Institution (USNM). This material consisted principally of exceptionally preserved Lower Devonian (Pragian) material from the Rhynie chert, Aberdeenshire, U.K. and Upper Carboniferous (Westphalian B) specimens from the British Middle Coal Measures and Westphalian D specimens from Mazon Creek, Illinois, USA, both in clay-ironstone nodules.

RESULTS AND DISCUSSION

Trigonotarbida and Anthracomartida

Trigonotarbids (Fig. 1, Figs. 2a, b) are superficially spider-like arachnids which ranged from the Upper Silurian (Přídolí) to the Lower Permian (Asselian). They are characterised by dorsal tergites divided into median and lateral plates and the presence of a locking ridge between the prosoma and opisthosoma. Of all the fossil arachnids, trigonotarbids are second only to scorpions in diversity and abundance and appear to have comprised much of the arachnid fauna during the Upper Carboniferous period. Some 75 species have been described of which fewer than 50 are probably valid.

Trigonotarbids were among the first fossil arachnids to be described. BUCKLAND (1837) described a fossil arthropod as a beetle, which was later recognised as an arachnid by WOODWARD (1871) who believed it to be a pseudoscorpion. KARSCH (1882) described another species, *Anthracomartus voelkelianus*, and established a new order Anthracomarti to accommodate these specimens along with material now recognised as phalangiotarbids (see below). SCUDDER (1884) retained Anthracomarti, though the order included fossil specimens now recognised as spiders, ricinuleids and phalangiotarbids. THORELL & LINDSTRÖM (1885) proposed Meridogastra as a replacement name for Anthracomarti on the grounds that the latter ordinal name was too similar to the generic name *Anthracomartus*. HAASE (1890) proposed a new classification in which he relegated Anthracomarti to a suborder of the Opiliones, though for the first time placed all the known anthracomartids in a single taxon with no incorrectly referred material. POCKOCK (1902) retained Anthracomarti as a suborder

of Opiliones, but discussed raising anthracomartids back to an order. FRIČ (1904) proposed a wide ranging classification of the fossil arachnids in which he reinstated Meridogastra, retaining it as an opilionid suborder, still containing ricinuleids and phalangiotarbids. Certain other fossil arachnids were placed in a suborder Pleur-araneae FRIČ, 1904, a division of the Araneae characterised by divided opisthosomal tergites. POCK (1910) pointed out the obvious similarities of the pleuraraneids to anthracomartids and synonymised Pleuraraneae with Anthracomarti. POCK (1911) re-established Anthracomarti as a distinct fossil arachnid order, noting that anthracomartids, phalangiotarbids and a new order Haptopoda might represent intermediates between opilionids and more primitive orders of arachnid. PETRUNKEVITCH (1913) retained Anthracomarti as a distinct order and PETRUNKEVITCH (1945) concluded that Anthracomarti were most closely related to spiders.

PETRUNKEVITCH (1949) radically changed this interpretation, dividing the arachnids into subclasses and splitting the Anthracomarti into two orders. Anthracomartida was retained for those forms with division of the tergites into five plates, i.e. the family Anthracomartidae. Anthracomarti was placed in a new subclass, Stethostomata Petrunkevitch, 1949, along with the monotypic fossil order, Haptopoda (see below). Stethostomata was diagnosed as arachnids with a broad prosoma-opisthosoma junction and downwards-hanging chelicerae. The remainder of the Anthracomarti were placed in a new order, Trigonotarbi Petrunkevitch, 1949, the sole representative of a new subclass, Soluta Petrunkevitch, 1949, defined by a prosoma-opisthosoma junction of variable width. This scheme was retained by PETRUNKEVITCH (1953, 1955) though in 1955 the ordinal names were changed to Anthracomartida and Trigonotarbida to fit nomenclatural conventions. Petrunkevitch's subclasses were followed by some authors (e.g. SAVORY, 1964), though his subclasses of Recent arachnids have not been widely adopted. However, palaeontologists continued to use his ordinal and supraordinal names for the fossil arachnids (e.g. GUTHÖRL 1964).

ZACHVATKIN (1952) included Anthracomarti in a superorder Actinoderma which also included Amblypygi, Araneae, Ricinulei, Opiliones and some of the Acari. DUBININ (1957) retained Soluta and placed Trigonotarbi in a class Arachnida, which for him also comprised spiders and opilionids. He did not place Anthracomarti in his scheme. SAVORY (1971) placed trigonotarbids and anthracomartids together in an infraclass Trigonotarboidea as part of a subclass Opilionomorphae which also included opilionids, ricinuleids, acarids and phalangiotarbids. FIRSTMAN (1973) placed Trigonotarbida and Anthracomartida in his pulmonate arachnids, i.e. those having book-lungs. VAN DER HAMMEN (1977) included Trigonotarbi and Anthracomarti with Araneae, Amblypygi, Uropygi and Schizomida in a taxon Arachnidea, though subsequently VAN DER HAMMEN (1989) omitted fossil orders from his scheme. GRASSHOFF (1978) placed Trigonotarbida close to Araneae, Amblypygi, Uropygi and Schizomida, but placed Stethostomata (including Anthracomarti) as much earlier derivative arachnids of a similar grade of organisation to palpigrades and phalangiotarbids.

The most important revision of Trigonotarbida was that of SHEAR & SELDEN (1986) and SHEAR *et al.* (1987) who criticised Petrunkevitch's diagnosis of Soluta and

argued that Trigonotarbida should be placed as the sister group of Araneae, Amblypygi, Uropygi and Schizomida; orders placed in a taxon Tetrapulmonata by SHULTZ (1990). SHEAR *et al.* (1987) argued that *Soluta* was diagnosed by Petrunkevitch on variable characters, i.e. prosoma–opisthosoma junction width and an opisthosoma of eight to eleven segments, which would suggest that *Soluta* was polyphyletic. Since the prosoma–opisthosoma junction is restricted in all trigonotarbids (SHEAR *et al.* 1987; DUNLOP 1994), *Soluta* is diagnosed on an incorrect morphological character and I follow these authors and reject *Soluta* as a higher taxon for Trigonotarbida. Trigonotarbida clearly belongs in Tetrapulmonata on the basis of two pairs of book-lungs, two-segmented clasp-knife chelicerae and a restricted prosoma–opisthosoma junction (see SHEAR *et al.* (1987) and SHULTZ (1990)) for further characters of Tetrapulmonata). DUNLOP (in press) has suggested the possibility that Trigonotarbida are a sister group of Ricinulei based on the synapomorphies of longitudinally divided tergites and a locking device between the prosoma and opisthosoma.

SHEAR *et al.* (1987) also questioned whether Anthracomartida could be retained as a distinct order from Trigonotarbida. PETRUNKEVITCH (1949, 1953, 1955) proposed a range of characters by which Anthracomartida differ from Trigonotarbida. These were the three-segmented, downwards-hanging chelicerae and broad prosoma–opisthosoma junction of the Stethostomata, three pairs of lung spiracles arranged parallel to the long axis of the body (rather than perpendicular to the axis as in other arachnids) and division of the tergites into five plates. PETRUNKEVITCH (1955) could only infer the presence of this third cheliceral segment and study of material in the BMNH has failed to substantiate either three-segmented chelicerae or three pairs of spiracles. Downward hanging chelicerae have also been identified in trigonotarbids (DUNLOP 1994). PETRUNKEVITCH (1949, 1955) regarded all anthracomartids as blind. In fact study of the best preserved anthracomartid material (e.g. BMNH I. 7893, In 15858, In 18333, In 22841, see also PETRUNKEVITCH (1949) fig. 202) revealed that there is every indication that anthracomartids are very similar to the Rhynie chert trigonotarbids in the family Palaeocharinidae (Dunlop, in prep.). Both have a similar box-shaped carapace with both median and lateral eyes (the eyes are symplesiomorphic) (Fig. 1), a locking ridge formed from tergite 1 which undertucks the carapace and similarly proportioned legs with a particularly short basitarsus. The dorsal opisthosomal segmentation of anthracomartids can be created simply by subdividing the lateral tergites and last dorsal tergite of a palaeocharinid (Fig. 1). I do not regard subdivided lateral tergites, in isolation, as a character of ordinal significance.

PETRUNKEVITCH's (1949) characters by which he split Anthracomartida from Trigonotarbida are therefore rejected as either misinterpretations of the fossils or as characters too trivial to be diagnostic of orders. No additional diagnostic characters for Anthracomartida were identified and the material comprising Petrunkevitch's order Anthracomartida represents a family within a unitary order, as it did prior to PETRUNKEVITCH (1949). There is a case for returning to KARSCH's (1882) original ordinal name Anthracomartida. However, since Petrunkevitch's Trigonotarbida embraced

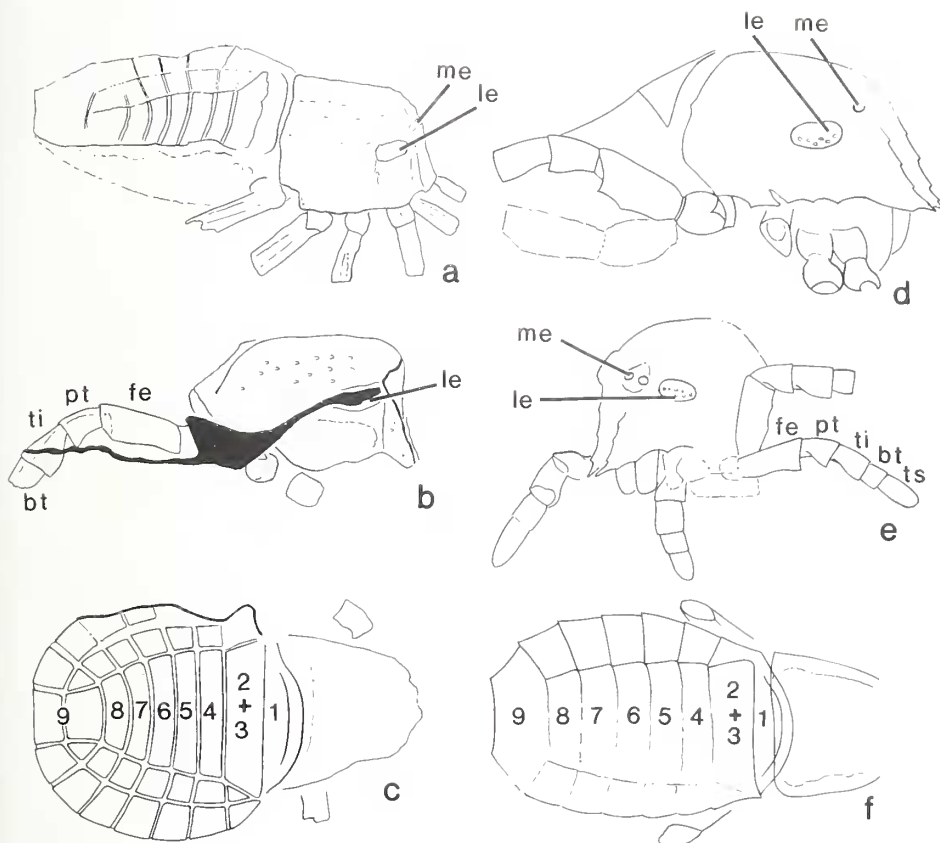


FIG. 1

Comparison of the morphology of palaeocharinid trigonotarbid and anthracomartids. Not to scale. a. *Cryptomartus priesti* redrawn from a latex cast of BMNH I. 15858 figured by PETRUNKEVITCH (1949, fig. 202). b. *Cryptomartus priesti* (BMNH I. 7893) showing a lateral eye tubercle and leg podomere proportions. c. *Cryptomartus priesti* (BMNH I. 15857) showing opisthosomal segmentation. d. *Palaeocharinus rlyniensis* (BMNH In 24673) showing eye tubercles. e. *Palaeocharinus* sp. (BMNH In 27752) showing eye tubercles and leg proportions. f. *Palaeocharinus* sp. (BMNH In 24674) showing opisthosomal segmentation. me = median eyes, le = lateral eyes, fe = femur, pt = patella, ti = tibia, bt = basitarsus, ts = telotarsus. Opisthosomal tergites numbered accordingly. The similar morphologies demonstrated here strongly suggest that palaeocharinids (Trigonotarbita) and anthracomartids (Anthracomartida) are closely related and argues for synonymising the two orders.

more of the material and has become better defined and more widespread in the literature (e.g. SHEAR *et al.* 1987) I prefer to retain this as the ordinal name and refer Anthracomartida to Trigonotarbida. Since anthracomartids are referred to Trigonotarbida (and hence Tetrapulmonata) and since Haptopoda is a distinct order in its own right (see below), Petrunkevitch's subclass Stethostomata becomes a polyphyletic grouping of a trigonotarbid family and a separate order. Retaining Stethostomata as a higher taxon for either Trigonotarbida or Haptopoda is unnecessary and I therefore propose that Stethostomata be rejected.

Phalangiotarbida

Phalangiotarbrids (Fig. 2c) are flattened, oval animals, with a semicircular carapace bearing six eyes on a single tubercle and an opisthosomal segmentation pattern of abbreviated anterior tergites and presumably fused posterior tergites. The sternites are longitudinally subdivided, with a ventral postabdomen at the posterior end of the opisthosoma (though considered dorsal by some authors (e.g. BEALL 1991)). The prosomal sternum is reduced and composed of three to five elements and the coxae are triangular, with evidence that the anterior coxae were movable and concealed the mouthparts. Autapomorphies of Phalangiotarbida have not been explicitly proposed, but would include an eye tubercle bearing six eyes, six abbreviated anterior tergites and reduced pedipalps and chelicerae. Phalangiotarbrids are restricted to the Westphalian stage and are rare. Some 26 species have been described, though this is an overestimate of their true diversity.

The first phalangiotarbid was described from Mazon Creek by SCUDDER (1868) as *Architarbus rotundatus* and identified simply as an arachnid. A second *Architarbus* species was described by WOODWARD (1872), who regarded it as probably being either an opilionid or amblypygid. KARSCH (1882) referred the genus *Architarbus* to his new order Anthracomarti (see above), a referral followed by SCUDDER (1884, 1890). HAASE (1890) introduced the name Phalangiotarbi as a suborder of Opiliones, distinct from Anthracomarti which he also regarded as an opilionid suborder (see above). However, HAASE (1890) only referred a new genus, *Phalangiotarbus*, to Phalangiotarbi, referring the other known phalangiotarbid genera to Architarbidae, which he considered a family of Amblypygi. FRIČ (1904) referred all the known phalangiotarbrids to a single taxon, Architarbidae, as a family within his opilionid suborder Meridogastra (see above). POCOCK (1910) questioned the opilionid status of phalangiotarbrids and POCOCK (1911) subsequently raised Phalangiotarbi to ordinal status.

PETRUNKEVITCH (1945) introduced a new ordinal name, Architarbi, in preference to Phalangiotarbi on the grounds that his new name was derived from better preserved material, i.e. the genus *Architarbus*. PETRUNKEVITCH (1948, 1949) commented that the architarbids had similar coxo-sternal regions to Cyphophthalmi (Opiliones) and suggested that cyphophthalmids were descended from architarbids, or at least shared a common ancestor with them. PETRUNKEVITCH (1949) referred Architarbi to his subclass Latigastra, which also included Scorpiones, Pseudoscorpiones,

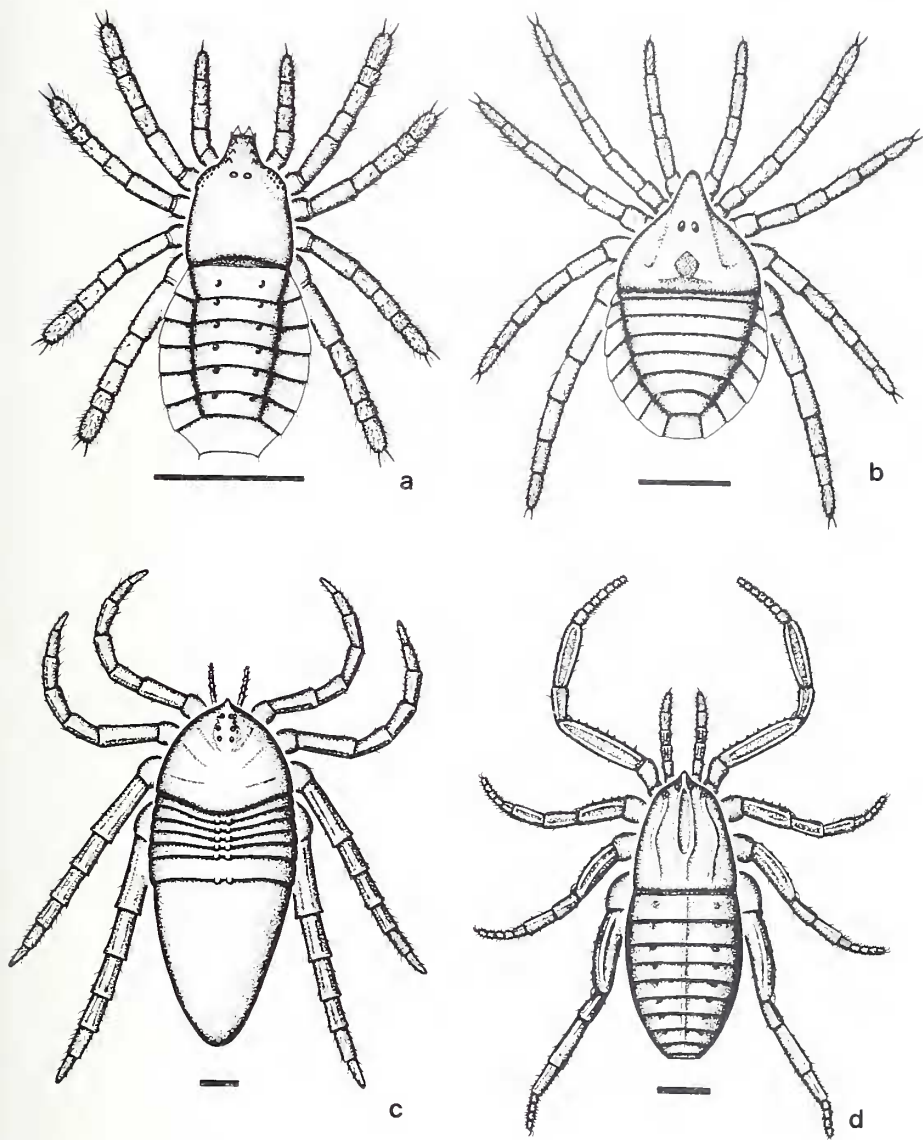


FIG. 2

Representative reconstructions of selected fossil arachnids. a. *Palaeocharinus rhytiensis* Hirst, 1923. (Trigonotarbida: Palaeocharinidae). Lower Devonian, Scotland. b. *Trigonotarbus johnsoni* Pocock, 1911. (Trigonotarbida: Trigonotarbidae) Upper Carboniferous, England. c. *Goniotarbus tuberculatus* (Pocock, 1911) (Phalangiotarbida: Architarbidae). Upper Carboniferous, England. d. *Plesiosiro madeleyi* Pocock, 1911 (Haptopoda: Plesiosironidae). Upper Carboniferous, England. Scale bars equal 2 mm.

Opiliones and Acari, all diagnosed by a broad prosoma–opisthosoma junction and forward-facing chelicerae. Architarbi was renamed Architarbida in 1955, although subsequent workers tended to use Architarbi. SAVORY (1971) referred Architarbi to an infraclass Opilionoidea, along with the Ricinulei, Opiliones and Acari. GRASSHOFF (1978) placed Architarbi as a relatively early derivative arachnid group of a similar grade of organisation to Pedipalpi and Stethostomata. VAN DER HAMMEN (1979) tentatively placed Architarbi with Ricinulei and Acari in a taxon Cryptognomae. KJELLESVIG-WAERING (1968) described a new phalangiotarbid, using the ordinal name Phalangiotarbida, as did BEALL (1991). SELDEN (1993) criticised Petrunkevitch's decision to substitute Architarbida for the perfectly good name Phalangiotarbida, retaining the latter name. I regard Phalangiotarbida as the correct ordinal name for these animals in preference to Architarbida.

The question of phalangiotarbid affinities has not been resolved, though the historical accounts of similarities between phalangiotarbids and amblypygids are superficial. PETRUNKEVITCH's (1948, 1949) hypothesis of phalangiotarbids being related to cyphophthalmid opilionids, deserves consideration, though this interpretation was based primarily on a general similarity of the coxo-sternal region. SHULTZ (1990) suggested that phalangiotarbids appear to have a postabdomen which would place them in his taxon Micrura (Tetrapulmonata + Palpigradi + Ricinulei + Acari). Kjellesvig-Waering in an unpublished, posthumous manuscript (see SELDEN, 1993) figured a chelicera in the holotype of *Geratarbus lacoei* (USNM 37966) from Mazon Creek. I have not seen this specimen, but its tiny chelicera was figured as a two-segmented clasp-knife chelicera similar to that characterising the Tetrapulmonata (see above). If true, clasp-knife chelicerae would be evidence for referring Phalangiotarbida to Tetrapulmonata. Phalangiotarbids also superficially resemble certain opilioacarids (DUNLOP 1995) in having abbreviated anterior opisthosomal tergites and indistinguishable posterior tergites. Opilioacarids should be considered in any future review of phalangiotarbid affinities. The nature of the respiratory organs and position of the gonopore in phalangiotarbids is unknown.

Haptopoda

The monotypic order Haptopoda (Fig. 2d) was created by POCOCK (1911) for nine specimens, all referred to *Plesiosiro madeleyi*, and all from the Upper Carboniferous of Coseley, Staffs., U.K. *Plesiosiro* is a flattened animal with a distinctive pattern of ridges on the carapace. It has relatively stout legs with small spines for prey capture on the femora. Leg 1 is longest and the tarsus is sub-divided into six joints. The tarsi of the other legs are sub-divided into four joints. The sternum is reduced and composed of two sclerites. POCOCK (1911) noted similarities between his new order and the Opiliones (i.e. a broad prosoma–opisthosoma junction, similar opisthosomal segmentation), Anthracomarti (i.e. an anal operculum (though this in fact a postabdomen in both orders)) and Uropygi (i.e. an elongate leg pair 1). PETRUNKEVITCH (1913) suggested that Haptopoda was probably synonymous with Phalangiotarbida, though subsequently he retained Haptopoda as a distinct order,

placing it with *Anthracomarti* in the subclass *Stethostomata* (PETRUNKEVITCH 1949, 1953, 1955) (see above). *Haptopoda* was renamed *Haptopodida* in 1955, though all subsequent authors have retained the name *Haptopoda* and I follow this convention. Subsequent studies have been vague in their placement of *Haptopoda* and most authors omitted it all together. FIRSTMAN (1973) and VAN DER HAMMEN (1977) both tentatively referred *Haptopoda* to what is now regarded as *Tetrapulmonata* and GRASSHOFF's (1978) placement of *Stethostomata* is noted above.

Phylogenetically the *Haptopoda* are still of uncertain affinity, as noted by POCKOCK (1911) in his original description, but may be related to either the *Opiliones* (SHEAR & KUKALOVA-PECK, 1990; W. Shear, pers. com.) or the *Tetrapulmonata*. If the latter case is true they might represent the sister group of *Pedipalpi* (*Amblypygi* + *Uropygi* + *Schizomida*) with which they share an elongate leg I and subdivided tarsi. However, neither the chelicerae or the respiratory organs, either of which could resolve the position of *Plesiosiro*, are preserved unequivocally. The status of *Haptopoda* as a separate order appears to be justified since its characters do not match the diagnoses of any other order, though its phylogenetic position remains equivocal. *Stethostomata* is rejected as discussed above.

Kustarachnida

The genus *Kustarachne* was established by SCUDDER (1890) for a monotypic species from Mazon Creek. SCUDDER (1890) referred this genus to *Anthracomarti*. MELANDER (1903) described two further species of *Kustarachne* from Mazon Creek (one of which was later identified as a ricinuleid (PETRUNKEVITCH, 1913)), again referring the genus to *Anthracomarti*. PETRUNKEVITCH (1913) described an additional Mazon Creek species and established a distinct order, also called *Kustarachne*, for the genus, characterised by immobile coxae surrounding a small sternum, fused palpal coxae, long, thin legs, chelate pedipalps, a pedicel and two eyes on a single tubercle. PETRUNKEVITCH (1949, 1953, 1955) placed *Kustarachne* (renamed *Kustarachnida* in 1955) close to *Uropygi* and *Schizomida* within a taxon, *Camarostomata*, based on the presence of fused palpal coxae (the *camarostome*) and chelate pedipalps. Subsequent classifications either placed *Kustarachnida* close to *Araneae* and *Amblypygi* (SAVORY 1971), tentatively close to *Solpugida* and *Pseudoscorpiones* (VAN DER HAMMEN 1977) or tentatively close to *Uropygi* (GRASSHOFF 1978). None of these schemes were particularly convincing. BEALL (1986) regarded Petrunkevitch's diagnostic characteristics for *Kustarachnida* of a pedicel, chelate pedipalps and fused palpal coxae as misinterpretations of the fossils, none of which are well preserved. BEALL (1986) suggested that because of the long slender legs, single pair of eyes and triangular coxae, *kustarachnids* are *opilionids*. Having examined the holotype of *Kustarachne temipes* (USNM 39767), I agree with these criticisms of Petrunkevitch's interpretations and the referral of this material to *Opiliones*. BEALL (1986) proposed that *Kustarachnida* be regarded as a *nomen nudum* and omitted from future phylogenies of the *Arachnida*, a view with which I agree.

SYSTEMATIC PALAEONTOLOGY

Class ARACHNIDA Lamark, 1801

Tetrapulmonata Shultz, 1990

Order Trigonotarbida Petrunkevitch, 1949

(Part) Anthracomarti Karsch, 1882: 560.

(Part) Meridogastra Thorell & Lindström, 1885: 31.

Opiliones, Suborder Anthracomarti Karsch; HAASE (1890): 650.

Opiliones, (Part) Suborder Meridogastra Thorell & Lindström; FRIČ 1904: 31.

Araneae, (Part) Suborder Pleuraneae Frič, 1904: 17.

Trigonotarbi Petrunkevitch, 1949: 235.

Anthracomartida Karsch; PETRUNKEVITCH 1955: 102.

Trigonotarbida Petrunkevitch; PETRUNKEVITCH 1955: 107.

Emended diagnosis. Tetrapulmonate arachnids with tergite 1 formed into a locking ridge, reduced in some families and tergites 2–8, 2–9 in some, divided into median and lateral plates. Tergites 2 and 3 fused into a diplotergite, tergites 4–9 not fused. Sternite 1 absent. Pedipalps and walking legs pediform. Chelicerae two-jointed and of the clasp-knife type.

Stratigraphic range. Silurian (Přídolí)–Permian (Asselian?).

Remarks. The clause in the diagnosis about unfused tergites recognises the division of tergites into median and lateral plates in ricinuleids.

Supraordinal position uncertain

Order Phalangiotarbida Haase, 1890

Opiliones, Suborder Phalagiotarbi Haase 1890: 650.

Opiliones, (Part) Suborder Meridogastra Thorell & Lindström; FRIČ 1904: 31.

Phalangiotarbi Haase; POCKOCK 1911: 45.

Architarbi Petrunkevitch, 1945: 1–72.

Architarbida Petrunkevitch; PETRUNKEVITCH 1955: 86.

Phalangiotarbida Haase; KJELLESVIG-WAERING 1969: 1280.

Emended diagnosis. Arachnids with a broad prosoma–opisthosoma junction. Carapace semicircular with six eyes on a single tubercle. Opisthosoma with abbreviated tergites anteriorly and fusion of segments posteriorly. Opisthosomal sternites longitudinally subdivided. Sternum reduced and composed of three elements. Chelicerae and pedipalps minute, walking legs stout and pediform.

Stratigraphic range. Upper Carboniferous (Westphalian A–D).

Order Haptopoda Pocock, 1911

Haptopoda Pocock, 1911: 41.

Haptopodida Pocock; PETRUNKEVITCH 1955: 100.

Emended diagnosis. Arachnids with a broad prosoma–opisthosoma junction. Carapace entire and ornamented with distinctive ridges, a pair of median eyes and a

pair of lateral eye tubercles present. Pedipalps pediform, leg I elongate and with tarsi subdivided into six joints, legs 2–4 with tarsi subdivided into 4 joints.

Stratigraphic range. Upper Carboniferous (Westphalian B).

***Nomen nudum Kustarachnida* Petrunkevitch, 1913**

Kustarachne Petrunkevitch, 1913: 71.

Kustarachnida Petrunkevitch; Petrunkevitch (1955): 100.

ACKNOWLEDGEMENTS

I thank Dr Richard Fortey (BMNH) and Jann Thompson (USNM) for the loan of material in their care and Dr Paul Selden, Prof. Bill Shear, Lyall Anderson and Simon Braddy for useful discussions. This work was initiated under a NERC studentship and completed under a NERC postdoctoral fellowship into early arachnid evolution.

REFERENCES

- BEALL, B. S. 1986. Reinterpretation of Kustarachnida (Abstract). *American Arachnology*, 34: 4.
- BEALL, B. S. 1991. The Writhlington phalangiotarbid: their palaeobiological significance. *Proceedings of the Geologists' Association*, 102: 161–168.
- BUCKLAND, W. 1837. The Bridgewater treatises on the power wisdom and goodness of God as manifested in the creation. Treatise IV. Geology and mineralogy considered with reference to natural theology. *William Pickering, London*.
- DUBININ, V. B. 1957. O novoi sisteme nadklassa Chelicerata. *Byulleten' Moskovskogo Obshchestva Ispytatelei Prirody, Otdel Biologicheskii*, 62: 25–33.
- DUNLOP, J. A. 1994. Palaeobiology of the Trigonotarbid Arachnids. *Unpublished Ph.D. thesis, University of Manchester*, 512 pp.
- DUNLOP, J. A. 1995. Are the phalangiotarbids just big opilioacarid mites? *Newsletter of the British Arachnological Society* 74: 8–9.
- DUNLOP, J. A. In press. Evidence for a sister group relationship between Ricinulei and Trigonotarbida. *Bulletin of the British Arachnological Society*.
- FIRSTMAN, B. 1973. The relationship of the chelicerate arterial system to the evolution of the endosternite. *Journal of Arachnology* 1: 1–154.
- FRIČ, A. Palaeozoische Arachniden. *Privately published by Anton Fric, Prague*, 80 pp.
- GRASSHOFF, M. 1978. A model of the evolution of the main chelicerate groups. *Symposium of the Zoological Society of London*, 42: 273–284.
- GUTHÖRL, P. 1964. Zur Arthropoden-Fauna des Karbons und Perms. 20. Neue Arachniden-Funde (Anthracom.) aus dem Westfal A des Aachner Karbons. *Paläontologische Zeitschrift*, 38: 98–103.
- HAMMEN, L. van der 1977. A new classification of the Chelicerata. *Zoologische Mededeelingen, Leiden*, 51: 307–319.
- HAMMEN, L. van der 1979. Comparative studies in Chelicerata I. The Cryptognomae (Ricinulei, Architarbi and Anactinotrichida). *Zoologische Verhandlungen*, 174: 1–62.
- HAMMEN, L. van der 1989. An Introduction to Comparative Arachnology, *SPB Academic Publishing, The Hague*, 576 pp.
- KARSCH, F. 1882. Über einige neue Spinnenthiere aus der Schlesischen Steinkohle und die Arachnoiden der Steinkohlenformation überhaupt. *Zeitschrift der Deutschen geolo-*

- gischen Gesellschaft* 34: 556–561.
- MELANDER, A. L. 1903. Some additions to the Carboniferous terrestrial arthropod fauna of Illinois. *The Journal of Geology* 11: 179–198.
- PETRUNKEVITCH, A. I. 1913. A monograph of the terrestrial Palaeozoic Arachnida of North America. *Transactions of the Connecticut Academy of Arts and Science* 18: 1–137.
- PETRUNKEVITCH, A. I. 1945. Palaeozoic Arachnida of Illinois. An enquiry into their evolutionary trends. *Illinois State Museum, Scientific Papers*, 3(2): 1–72.
- PETRUNKEVITCH, A. I. 1948. The case of *Phalangiotarbns subovalis* Woodward. *American Journal of Science* 246: 353–362.
- PETRUNKEVITCH, A. I. 1949. A study of Palaeozoic Arachnida. *Transactions of the Connecticut Academy of Arts and Science* 37: 69–315.
- PETRUNKEVITCH, A. I. 1953. Palaeozoic and Mesozoic Arachnida of Europe. *Memoir of the Geological Society of America* 53: 1–128.
- PETRUNKEVITCH, A. I. 1955. Arachnida. pp. 42–162. In: *Treatise on Invertebrate Palaeontology*, part P. Arthropoda 2. (R. C. MOORE, ed.). *Geological Society of America and University of Kansas Press. Boulder, Colorado and Lawrence, Kansas*, 181 pp.
- POCOCK, R. I. 1910. Notes on the morphology and generic nomenclature of some Carboniferous Arachnida. *Geological Magazine* 5: 505–512.
- POCOCK, R. I. 1911. A monograph of the terrestrial Carboniferous Arachnida of Great Britain. *Monograph of the Palaeontographical Society*, 84 pp.
- SAVORY, T. H. 1964. The Arachnida. *Academic Press, London*, 291 pp.
- SAVORY, T. H. 1971. Evolution in the Arachnida. *Marrow Monographs, Marrow, Watford*, 42 pp.
- SCUDDER, S. H. 1868. Supplement to descriptions of Articulates. Description of fossil insects found on Mazon Creek and near Morris, Grundy Co., Ill. *Geological Survey of Illinois* 3: 566–572.
- SCUDDER, S. H. 1884. A contribution to our knowledge of Palaeozoic Arachnida. *Proceedings of the American Academy of Arts and Science* 20: 15–22.
- SCUDDER, S. H. 1890. Illustrations of the Carboniferous Arachnida of North America. *Memoirs of the Boston Society of Natural History* 4: 443–456.
- SELDEN, P. A. 1993. Fossil arachnids-recent advances and future prospects. *Memoirs of the Queensland Museum* 33: 389–400.
- SHEAR, W. A. & KUKALOVA-PECK, J. 1990. The ecology of Paleozoic terrestrial arthropods: the fossil evidence. *Canadian Journal of Zoology* 68: 1807–1834.
- SHEAR, W. A. & SELDEN, P. A. 1986. Phylogenetic relationships of the Trigonotarbida, an extinct order of arachnids. *Actas X Congreso Internacional de Arachnologia, Jaca, España*, 1986, 1: 393–397.
- SHEAR, W. A., SELDEN, P. A., ROLFE, W. D. I., BONAMO, P. M. & GRIERSON, J. D. 1987. New terrestrial arachnids from the Devonian of Gilboa, New York (Arachnida, Trigonotarbida). *American Museum Novitates* 2901: 1–74.
- SHULTZ, J. W. 1990. Evolutionary morphology and phylogeny of Arachnida. *Cladistics* 6: 1–38.
- THORELL, T. & LINDSTRÖM, G. 1885. On a Silurian Scorpion from Gotland. *Kungliga Svenska Vetenskapsakademiens Handlingar* 21: 1–33.
- WEYGOLDT, P. & PAULUS, H. F. 1979. Untersuchen zur Morphologie, Taxonomie und Phylogenie der Chelicerata. *Zeitschrift für Zoologie, Systematik und Evolutionsforschung* 17: 85–200.
- WOODWARD, H. 1871. On the discovery of a new and very perfect arachnide from the ironstone of the Dudley Coal-field. *Geological Magazine* 8: 383–387.
- WOODWARD, H. 1872. On a new arachnide from the Coal-measures of Lancashire. *Geological Magazine* 9: 385–387.
- ZAKHVATKIN, A. A. 1952. Razdeleniye kleschchei (Acarini) na odryady i ikh polozheniye v sisteme Chelicerata. *Parazitologicheskii Sbornik. Institut Zoologii. Akademiyia Nauk Gruzinskoi SSR* 14: 5–46.